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COMMENTARY

SONG SIMILARITY IN POPULATIONS OF FOX SPARROWS: A REJECTION OF NAUGLER'S AND SMITH'S CONCLUSIONS

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Naugler and Smith (1991) used data on song in Fox Sparrows (*Passerella iliaca*) to test hypotheses about the evolution of the structure of song in insular avian populations. Their conclusions are incorrect for a host of reasons. The authors appear to have misused or ignored information within the references they cite and they appear to have relied on second-party assessments (Miller 1982) of data within these references. It will become clear that the review process for this manuscript failed in its assessment of the manuscript's accuracy and its contribution to ornithology.

Naugler and Smith presented two hypotheses concerning possible effects of insularity on song complexity: (1) The song complexity hypothesis predicts song in insular populations may become more complex than mainland populations due to weaker selective pressures resulting from reduced interspecific constraints (competitive release ?). (2) The founder effect hypothesis predicts song complexity may be less in insular than mainland populations if a "bottleneck" develops during the founding of the population. A bottleneck would result in an incomplete sampling of mainland song complexity, thus, exposing future generations to a depauperate species specific auditory field from which to model song.

Following the procedures for measuring song complexity presented by Miller (1982), Naugler and Smith generated statistics for four measures of song complexity from their study population of migratory Fox Sparrows on Bon Portage Island, Nova Scotia. These were: (1) size of song repertoire (number of structurally distinct song units sung by an individual), (2) number of syllables/song, (3) number of syllable types/song, and (4) syllable diversity [number of different syllables (syllable types) in a song/total number of syllables in a song]. They then tested the two hypotheses by comparing their statistics with what they assumed to be similar statistics they or Miller (1982) generated from two other non-isolated Fox Sparrow populations reported on by Martin (1977, 1979) and Blacquiere (1979). In brief, these comparisons led them to conclude that song complexity was less in the Bon Portage population and that this condition resulted from a bottleneck effect.

Naugler and Smith (1991:1003) began by inferring incorrectly that the Fox Sparrow populations studied by Martin and Blacquiere were "resident populations." I clearly stated that "the Fox Sparrows I studied began singing within a few days of their arrival on the breeding areas (late March through April)" (Martin 1977: 210). Blacquiere (1979:10) began his *Results* with, "In eastern Newfoundland the Fox Sparrow is one of the earliest spring migrants to return from its wintering ground."

In laying the groundwork for their acceptance of a bottleneck hypothesis Naugler and Smith contend that their data represented birds more geographically/behaviorally isolated than those studied by myself or Blacquiere. They contend (p. 1002) that the Martin/Blacquiere populations were "non-isolated" and, further, that ". . . of all these populations only Bon Portage is at the range limit and has no nearby populations to facilitate gene flow." Both my publications (referenced by the authors) described my populations as geographically "distinct," populations in which ". . . no continuous band of breeding birds connects the three populations . . ." (Martin 1977:209, 1979:173). Insularity and the effects of habitat islands in many Great Basin species are well described phenomena (e.g., see Cody and Diamond 1975; Brown 1971, 1978). Genetic and behavioral isolation of montaine populations does not *a priori* differ from that observed in near-mainland oceanic island populations. Further, the data sets Naugler and Smith used from Blacquiere's study represented two island populations located off the east coast of Newfoundland. Why the authors do not assume Fox Sparrows breeding on islands located on the eastern fringe of Newfoundland to be at the limit of the species' geographic range escapes me. Granted the Atlantic Ocean is a geographic barrier and not a biotic one, but the population nonetheless is at its eastern spatial limit.

The authors also support their claim of bottleneck effects with the contention that significantly more genetic exchange may occur in (or between) the populations studied by Martin and Blacquiere and their neighboring populations than may have occurred in their study population. This contention was based on the high inter-year site fidelity demonstrated by a few breeding birds they had banded. However, both Martin (1977:215) and Blacquiere (1979:11) stated that all birds (few that there were) that they had banded one year and relocated the next had returned to the same area of occupancy. Again, there is no empirical site fidelity data justification for them (p. 1003) to assume their study population has remained any more "effectively isolated" than those populations used for comparison.

The authors make multitudinous errors regarding the parameters of song they used for comparison. They incorrectly compared as synonymous those units of sound they defined as syllable types/syllables with what I defined as syllable-types. They defined syllable types (syllables) as ". . . a sound or series of sounds preceded and followed by a silent interval of at least 10 msec

. . ." (p. 1002). I defined syllable-types ". . . as the single- or multi-noted sounds, which may or may not be repeated . . . may be present or absent, uttered singly or repeated in a particular song-type, but never fragmented so that only a portion of it would be in evidence" (Martin 1977:212). Thus, two sound units that were structurally different in frequency, each preceded and followed by 10 msec of silence yet always linked together by usage would have been classified as two different syllables (syllable types) by Naugler and Smith, but as one syllable-type by me.

Naugler and Smith (1991:1001, Table 1) incorrectly presented data concerning "Syllables in Population" which they specifically referenced to my 1977 paper. They indicated that my Cub River population possessed a (mean) repertoire of 48.5 syllables whereas the two populations from Blacquiere's study possessed 37 and 42. My 1977 paper did not present any data sets that were differentiated at the level of individual canyon population. The Appendix of Martin (1979:177) did list the "percent of Fox Sparrows that possessed a particular syllable-type" both by year and by canyon population. But, these data showed that the Cub River birds possessed 36 and 39 syllable-types in 1973 and 1974, respectively. Cub River birds possessed only 39 of the possible 49 syllable-types represented by all three canyon populations. (Martin's Blacksmith Fork Canyon populations also did not demonstrate the full complement of 49 syllable-types in either 1973 or 1974.) Thus, the conclusion presented by their Table 1 that the number of syllables in the population was greater in Cub River birds than those studied by Blacquiere was incorrect.

The inability to compare syllables/syllable-types between these studies is further exacerbated by differences in what each researcher has considered allowable syllable type variation. Comparison of figures illustrating syllable-type variation allowed by Martin (1977, Fig. 4) with that allowed by Blacquiere (1979, Fig. 11) shows that Blacquiere designated syllables as different types based upon structural differences that I would have considered minor. He described many syllables, whereas I would have described but a few, with each syllable-type possessing significant variability. Overall, then, comparisons between these three studies at the level of numbers of syllables in population, syllable types, etc. are not valid. Any conclusions about song complexity drawn from measures of numbers of syllable or syllable diversity are questionable.

Perhaps the most grievous error of Naugler and Smith was their apparent reliance on values presented by Miller (1982) purportedly reflecting the content of my papers. This action resulted in their (p. 1002, Table 1) listing the mean Number of Syllables per Song as 8.2 and mean number of Syllable Types per Song as 8.2 for each canyon population I studied (Martin 1977). Although the authors referenced these data to my 1977 publication, nowhere in that publication do I present such data.

Syllable (syllable type) as used by Naugler and Smith (or Miller) and syllable-type as used by Martin are very different parameters of song. Martin (1977:213, Table 2) listed only "syllable-types composing particular song-types", not syllables composing songs as listed by the other authors. I clearly stated (Martin 1977:212) that songs were analysed ". . . on the bases of their constituent syllable-types. Syllable-types were defined as the single- or multi-noted sounds . . . could be uttered singly or repeated in a particular song-type." Those values listed in text, in Table 2 and in the Appendix of Martin (1977) represent syllable-types per song. Actual number of syllables per song was never listed in my publications. Where do these values come from?

Such values could only be generated by erroneously computing them oneself, as did Miller in 1982, or by misinterpreting my definition of syllable-types. (Miller's publication is the only published reference, with which I am familiar, that lists such values.) I had written to Miller about his misrepresentation of my data in the early 1980s. His reply was to the effect that, with regard to his usage of the data, the error did not significantly alter his conclusions. He did not believe an erratum was warranted. Unfortunately the use to which Naugler and Smith put these values does significantly impact their conclusions.

The distinction between my use of the terms syllables per song and syllable-types per song is most important. A song consisting of syllable sequence 1, 11, 34, 34, 35, 29, 37, 38, 38, 38, 38 (illustrated in Figure 3, Martin 1977:212) was listed as 1, 11, 34, 35, 29, 37, 38. The song contained 11 syllables, but only 7 syllable-types. Such a song would have a syllable diversity value of 0.64. Naugler and Smith (after Miller 1982) listed the number of syllables per song and syllable-types per song both as 8.2 for my populations. This resulted in an incorrect syllable diversity value of 1.0.

Analysis of song parameters from 25 birds randomly drawn from the 1974 populations reveals the following values: number of syllables per song = 11.97 ± 2.09, number of syllable-types per song = 8.66 ± 1.6 and syllable diversity per song = 0.73 ± 0.12. Thus, syllable diversity in Utah/Idaho birds is lower than that found in the Canadian birds, not higher as reported by Naugler and Smith.

This same type of error occurs in their reference to number of songs per individual. Miller (1982) and Naugler/Smith (Table 1, p. 1001) treat as similar the categories of songs and song-types when comparing their data to mine. In my study, "although songs of individuals may be designated the same type, this does not imply that these songs are structurally identical. All the major song-types were represented by a large variety of song-versions" (Martin 1977:212). This "distinction between Fox Sparrows, major song-types and songs is important as the distinction between syllables and syllable-types. Individual birds could possess a repertoire containing more than one version of one of the major song-types listed in the Appendix . . ." (Martin 1977:214). As a result of this methodology the 25 bird sample from 1974 had computed means of 2.68 ± 0.55 and 2.96 ± 0.6 for numbers of songs and song-types per bird, respectively. This resulted in a song complexity value of 0.92 ± 0.14, less than the 1.0 computed for the eastern Canadian birds. (The values for all 63 birds from 1974 were: songs = 3.1 ± 0.81, song-types = 2.76 ± 0.64 and song diversity = 0.90 ± 0.16.)

In summary, Naugler and Smith's conclusions are incorrect because their assumptions do not accurately reflect the data bases they use for comparison. Varia-

tion based upon numbers of syllables per individual are not necessarily less in the Bon Portage birds. Syllable types were not defined/identified similarly in the three studies and, therefore, are noncomparable. There is little justification to assume males in Blacquiere's population had fewer syllables per song than the birds I studied. Not knowing exactly how Naugler and Smith identified and separated syllable types makes uncertain any inter-study comparisons based on values for numbers of syllables per song and syllable types per song. Accepting, however, their assessment as correct (Bon Portage males have fewer syllables and syllable types per song than males in the other populations), their error in following Miller's lead in misconstruing my data invalidates their assessment that Utah/Idaho males have a syllable diversity (1.0 rather than the true 0.74) greater than the Canadian birds. Further, their contention that the number of songs per male and by inference song complexity (songs/song types) were both greater in Utah/Idaho birds is false. Utah/Idaho males did possess a greater number of songs per individual, but their song complexity value (0.91) is less than that for Canadian birds (1.0). These assessments of complexity are central to their argument that Bon Portage birds have been effected by a bottleneck which resulted in depauperate syllable (and song) diversity. Lastly, Naugler and Smith's contention that Blacquiere's and my studies dealt with "resident populations" was false.

There is little to support the conclusions of Naugler and Smith. Their assessment of the selection pressures and historical events which have resulted in the pattern of syllable and song repertoire organization in Fox Sparrows must be rejected. The problems with this publication discussed herein beg comment regarding the failure of our manuscript review process. However, all I shall say is whomever reviewed this manuscript should have been knowledgeable enough about vocal behavior and geographic distribution in the *Passerella–Melospiza–Zonotrichia* complex to know which populations (races) were resident and which were migratory.

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SIMILARITY BREEDS CONFUSION: A REPLY TO MARTIN

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Martin (1993) has recently criticized a short communication describing the song structure of a population of Fox Sparrows *Passerella iliaca* (Naugler and Smith 1991). Contrary to Martin's assertion, the purpose of this paper was not to "test hypotheses about the evolution of the structure of song" but was rather more modest. We presented a descriptive study of song in an insular population and suggested that the observed patterns were consistent with the "founder effect hypothesis." We suggested that such an effect need not occur only when a population is founded, but also in small isolated populations where periodic bottlenecks could occur after seasons of high mortality. It will become apparent that while our original paper did contain several errors, the criticisms raised by Martin are either inaccurate or do not greatly change the trends reported by us, and that Martin's disparagement of the editorial review process is, perhaps, not deserved in this instance.

Martin's first criticism results from an unfortunate misreading of our original paper. He claimed that we incorrectly concluded that the populations of Fox Sparrows studied by him (Martin 1977, 1979) and Blacquiere (1979) were resident. When we stated that "the studies cited at the *outset* of this paper all deal with resident populations" (Naugler and Smith 1991:1003), we were referring to the papers cited in the opening paragraph of our study (i.e., Nottebohm 1969, Thielcke 1973, Mundinger 1975, Mirsky 1976, Baptista and Johnson 1982, Lynch and Baker 1986, Baker and Jenkins 1987), not to the work of Martin and Blacquiere which we first cited almost two pages later. Martin (1977) and Blacquiere (1979) both clearly state that the Fox Sparrows they studied were migratory.

Secondly, Martin has objected to our argument that the population described by Naugler and Smith (1991) was more isolated than the populations studied by Martin and Blacquiere. Martin has missed our point. We did not argue that the previously described populations were not "geographically distinct." Indeed "we